THE ROLE OF THE VOCALIZATION OF HARBOUR SEAL (PHOCA VITULINA) PUPS IN PREVENTING SEPARATION FROM THEIR MOTHERS

ELIZABETH ANNE PERRY

THE ROLE OF THE VOCALIZATION OF HARBOUR SEAL (Phoca vitulina) PUPS IN PREVENTING SEPARATION FROM THEIR MOTHERS

BY

© ELIZABETH ANNE PERRY, B.A. (Honours)

A Thesis Submitted to the School of Graduate Studies
in Partial Fulfillment of Requirements for the Degree of
Master of Science

Departments of Biology and Psychology
Memorial University of Newfoundland
August, 1986

St. John's Newfoundland

ISBN 0-315-33626-9

ABSTRACT

Interactions between harbour seal (*Phoca vitulina concolor*) mothers and pups were observed, and recordings were made of pup vocalizations, on the island of Miquelon near southeastern Newfoundland, Canada. Pup vocalizations were individually distinct on the basis of several physical parameters, most importantly the frequency of the major harmonic. These data and analyses of contextual variables indicated that the mothers might use these vocalizations for individual recognition of their offspring and for ensuring that contact is maintained. Calls can be transmitted simultaneously in air and underwater and it is hypothesized that differences between these versions of the calls increase the accuracy with which the mothers can localize their pups.

ACKNOWLEDGEMENTS

I wish to thank my supervisor, Dr. Deane Renouf, for her kind support, guidance and encouragement throughout all stages of this thesis.

I also extend thanks to the members of my advisory committee, Drs. Daniel Stewart and Anne Storey, for their patience and insightful reviews of the manuscript.

Great appreciation is extended to John Lawson who could anticipate and smooth any difficulties with ingenious methods, Nicole Roy for her motivating influence and John Piatt for knowing when a break was necessary.

Field research on Miquelon was made easier through the friendship and constant assistance of Alain Desbrosse and Roger Etcheberry. The moral support of Monsieur Marcel Dagort shall never be forgotten.

My deepest appreciation goes to my father, Mr. F. Robert Perry, and my grandmother, Mrs. Freda Perry, who never lost confidence in me.

Financial support was kindly provided by a Marine Sciences Research Laboratory scholarship and a Memorial University of Newfoundland bursary.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER ONE: INTRODUCTION

The purpose of this study was to investigate the possibility that female harbour seals (*Phoca vitulina concolor*) can distinguish their pups from others based on call structure and to examine how females use the call to monitor their pups' movements.

Phocids give birth on land or ice to offspring which, in many species, remain there until they are weaned. The cows which leave the nursery areas, on their return, are faced with the task of relocating their pups. Harp seals (*Phoca groenlandicus*; Terhune et al., 1979), ribbon seals (*Phoca fasciata*; Burns, 1981), Baikal seals (*Pusa sibrica*) and ringed seals (*Pusa hispida*; Frost and Lowry, 1981) give birth on sea ice to young with white pelage. These well camouflaged pups are frequently left alone on the ice while their mothers go to sea. Upon return the cows must relocate their young and probably do so on the basis of features of the birth place rather than those of the pup (Terhune et al., 1979). Other seals, such as southern (*Mirounga leonina*; Ling and Bryden, 1981) and northern (*Mirounga angustirostris*; Le Boeuf et al., 1972) elephant seals and grey seals (*Halichoerus grypus*; Bonner, 1981) congregate on beaches or rocky shores[1] in large herds for parturition and these cows must be able to distinguish their offspring from the many others in the herd. The female northern elephant seal relies, in part, on the call of her young to do this. When she wishes to reunite with her pup after a separation, she emits a "pup attraction call" (PAC) to which

[1]Breeding southern elephant seals also occur on land-fast ice in their most southerly ranges (Ling and Bryden, 1981) and breeding grey seals are also found on pack ice in the Baltic Sea (Curry-Lindahl, 1975) and in the Gulf of St. Lawrence (Mansfield and Beck, 1977).

the young responds vocally (Bartholomew and Collias, 1962). Petrinovich (1974) demonstrated that female northern elephant seals are able to distinguish their offspring from others on the basis of their calls. Using playback techniques, he found that mothers emitted the PAC significantly more often to their own pups' cries than to those of alien young. Similar behaviour has been documented in Otariidae. Trillmich (1981) demonstrated that Galápagos fur seal (*Arctocephalus galapagoensis*) pups respond vocally to the PAC of their mothers. The same has been suggested for South American sea lions (*Otaria flavescens*; Vaz-Ferreira and Achaval, 1979). Therefore, it appears that the vocalizations of the young play a significant role in maintaining or establishing mother-offspring contact for those pinnipeds which have been studied.

Unlike most other phocids, the harbour seal pup regularly follows its mother into the water soon after birth. The pair spends a relatively small amount of time on beaches or rock ledges where they nurse or sleep, their remaining time being spent in the water. Since they travel together the mother is not usually faced with the task of relocating her pup, but must instead maintain contact with it. The waters surrounding the haul-out sites often have poor visibility, strong currents and high ambient noise levels which could increase the risk of separation for the mother and her young. To maintain contact, at least one member of the pair must be able to monitor the movements of the other. This cannot always be done visually. The mother usually moves in front of her pup and, therefore, cannot continuously watch it. Further, both mothers and pups are visually restricted by the turbidity of the water.

Harbour seals emit aggressive growls and underwater clicks (Renouf and

Davis, 1982; Schusterman, et al., 1970), but females apparently have no counterpart to the PAC of other species. The offspring, on the other hand, are quite vocal, emitting brief sheep-like bleats. They make this cry until they are weaned when it disappears from their repertoire[2], which suggests that it serves some function in the nurturant relationship. The frequent calling of the young might provide a cue by which the mother could monitor the movements of her pup. If, as is often the case, pups are vocalizing in close proximity it would also be useful if females could distinguish their own offsprings' calls. There is some evidence to suggest that this might be so. Renouf (1984) suggested that calls of pups differed enough in fundamental frequency to enable individual identification by mothers. The calls also seemed to differ individually on the basis of harmonic interval, duration of the call, and rate and range of frequency modulation. However, these results were obtained from a small number of pups. Renouf (1985) recently demonstrated that a captive, adult female harbour seal was able to discriminate between recorded calls of different pups. Even if the mother could potentially confuse her pup's cry with those of others, she normally has an additional cue in that the call of her pup would be the closest one since the youngster is predisposed to follow its mother (Lawson, 1983). However, in situations such as when a disturbed herd flees into the water, proximity is an unreliable indicator of pup identity. In such circumstances individually distinctive calls would be important in helping separated mothers and pups reunite.

Renouf (1984) also found that pups can transmit calls simultaneously in air

---

[2]There is evidence to suggest that some captive harbour seals occasionally continue to vocalize after weaning(Ralls et al., 1985).

and underwater. She found that vocalizations differed in fundamental frequency and harmonic distribution between the two media. If these preliminary results are reliable then simultaneous versions of the call could provide valuable information to the mother. For example, if a female could not to hear the airborne cries of her pup due to high ambient noise levels she could rely on the underwater version. Further, a comparison of the binaural arrival time differences between the aerial and underwater vocalizations could supply precise distance information to the mother to help her locate her calling offspring.

This study was designed to test for the existence of physical differences among pup voices, and to further compare the air and water versions of the calls. Contextual data were recorded to ascertain if maternal behavioural changes were associated with changes in the physical characteristics of the calls.

CHAPTER TWO: METHODS

Preliminary work for this thesis was carried out during the summer of 1983 and the data described herein were gathered during the summer of 1984.

Observation methods and apparatus

Between May and August, a herd of more than 600 harbour seals congregate in the Grand Barachois of Miquelon (45° 45′N and 56° 14′W), a French island 19 kilometers from the southeastern coast of Newfoundland, Canada. The Barachois is a large tidal lagoon with a sandbank in the center which becomes exposed as the tide ebbs. The seals haul out on the sandbank as the water falls and leave again when the tide rises.

The seals haul out on this three square kilometers of sand in four discrete groups. One group, the nursery (Figure 1), forms during the last two weeks of May and is composed of approximately 40 pairs of mothers and pups. Though many of these animals were unidentified during this study, the 10 that were recognizable, on the basis of pelage markings, used this nursery site exclusively during all observed haul outs.

A blind was erected on the nursery approximately 10 meters from the water's edge at low tide (see Figure 1). It faced a shallow channel which the seals used to enter and leave the nursery. The blind consisted of a rectangular canvas housing placed over an aluminium frame, 1.5 meters in height, secured to a one-square-meter base mounted on four steel legs 1.5 meters long (Figure 2). Tire rims welded to each leg were buried in the sand to increase the blind's stability.

Figure 1: A map of the islands of Miquelon and Langlade with an enlargement showing details of the Grand Barachois and the location of the nursery blind.


100 M
-SAND FLATS
-GOULET
★- NURSERY BLIND

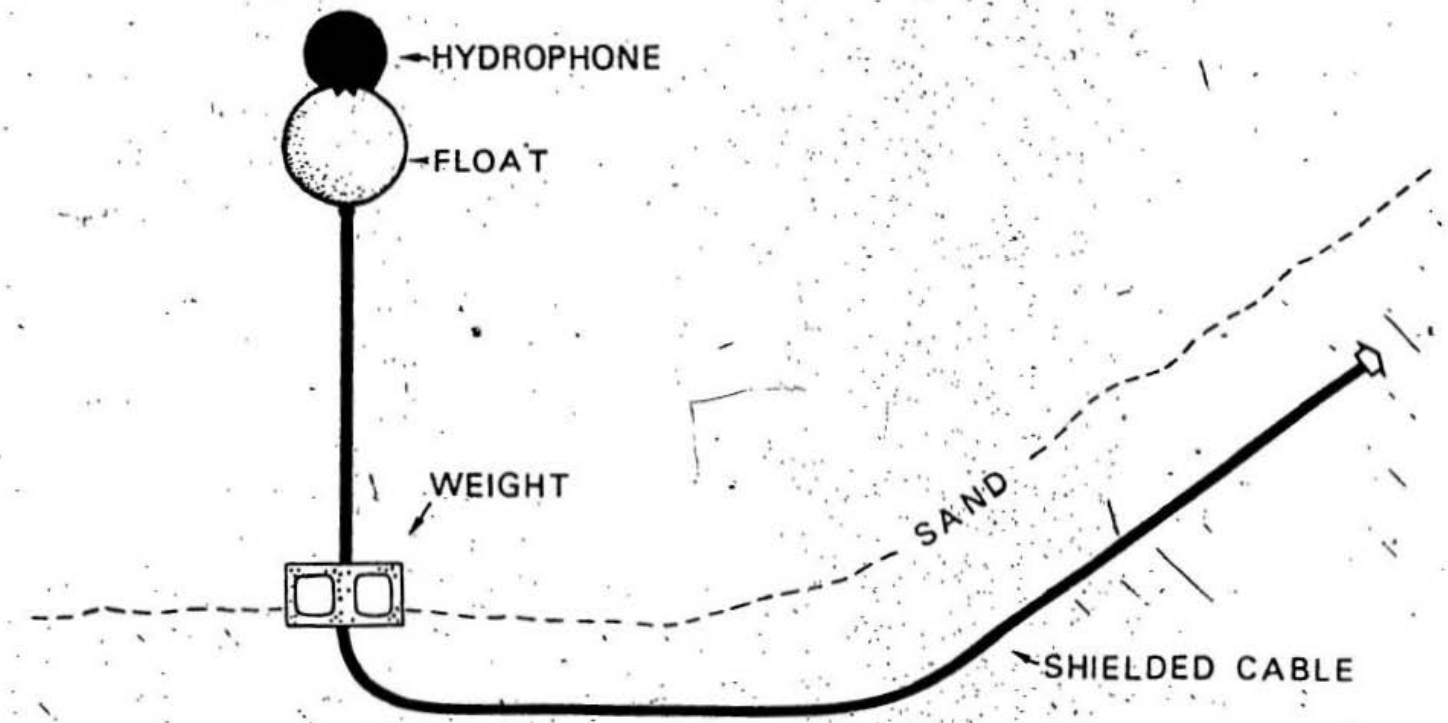
Figure 2: Elevated observation blind.

There were three 0.6 by 0.6 meter vinyl windows in the blind which could be opened. This blind had been in place during three consecutive breeding seasons (1981-1983) and there was no evidence that it was disruptive to the seals. During this study, mother-pup pairs often passed directly under the blind when travelling across the sand flats.

The observer entered the blind prior to peak high tide and set up equipment before the seals began to haul out. Tape recordings of the aerial and underwater versions of pup calls were made between commencement of the haul out and the reversal of the tide. Calls were recorded using a four-channel Uher 4400 Report model reel-to-reel tape recorder. The aerial signals were received by a Dan Gibson P200 parabolic microphone and the underwater calls by a Gould CH17U hydrophone. The parabolic microphone was mounted on a tripod in the blind and the hydrophone was permanently anchored in the middle of the channel near the blind. The transducer was floated in the water by a cork, 10 centimeters in diameter, so that it was one meter above the bottom and one meter below the surface at low tide (Figure 3). A 70 meter length of shielded cable connected the hydrophone to the Uher recorder and was buried 20 centimeters below the sand to reduce acoustic noise or disturbances created by the movement of seals across the sand.

Underwater sounds were monitored using Realistic miniature Nova 35 stereo headphones to detect the beginning of calling bouts originating underwater. Aerial calls also could be heard while the headphones were in use. Recording started immediately when a call was heard in air or underwater. At the same time the pup was assigned an identification number and the following contextual data were collected:

Figure 3: Drawing of underwater hydrophone recording station set up in the shallow channel in front of nursery area.


HYDROPHONE
FLOAT
WEIGHT
SAND
SHIELDED CABLE

1. The approximate distance (in m) of the pup from its mother at the time it was calling (Figure 4). When a pup did not seem to be accompanied by its mother, and when the pup's approaches were repeatedly rejected by any nearby females, it was designated as a lone pup.

2. The position of the mother's head relative to the surface of the water during the calling bout. The three categories were: completely visible above the surface of the water, partially submerged, and submerged (Figure 5).

3. The occurrence of any nose-to-nose contact between the mother and pup.

4. The mother's response to her pup's calls as measured by changes in her direction of movement, either toward her pup, away from her pup, or no movement.

Sonagraphic analyses

A call was considered to be one vocalization; calling bouts contained from one to 26 consecutive calls. The first call in a sequence was considered to be the start of a calling bout and the bout ended when the pup either stopped calling or followed its mother onto the sandbank, thus preventing simultaneous recording.

The calls were analyzed with a Kay 6061B Spectrum Analyzer using the wide band filter setting. The frequency scale was calculated in 20 Hz intervals. The following variables (illustrated in Figure 6) were measured from the sonagraphs:

1. **Duration of call**; the distance between the onset and termination of the longest harmonic within the call (to the nearest 0.1 seconds).

2. **Inter-call interval**; the time interval between calls measured from the termination of one call to the onset of the next call (to the nearest 0.1 seconds).

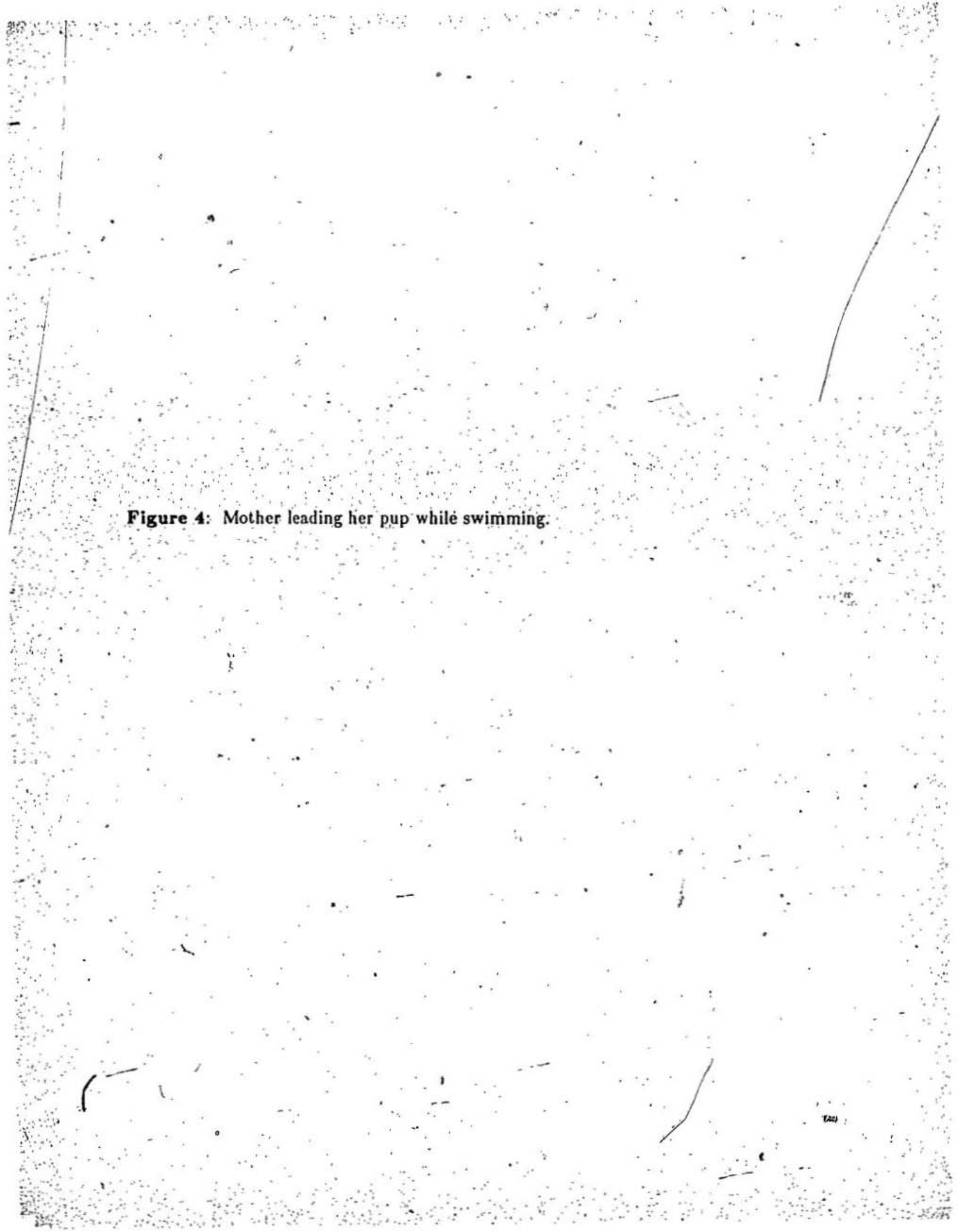
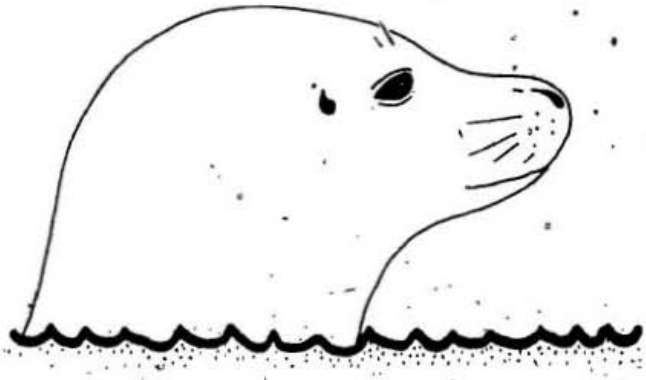
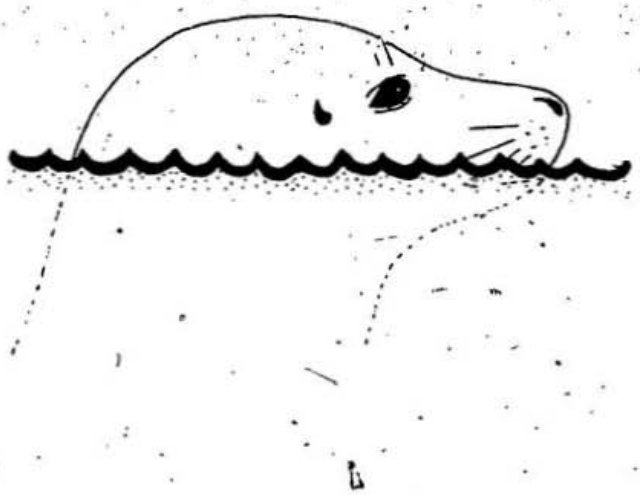


Figure 4: Mother leading her pup while swimming.

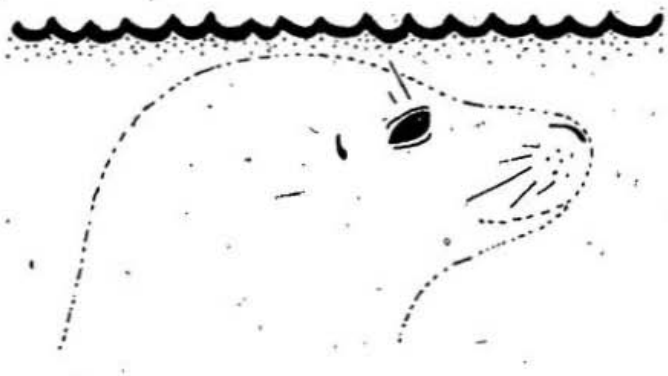
Figure 5: Schematic diagram showing the three categories of the position of the mother's head.



POSITION 1



POSITION 2



POSITION 3

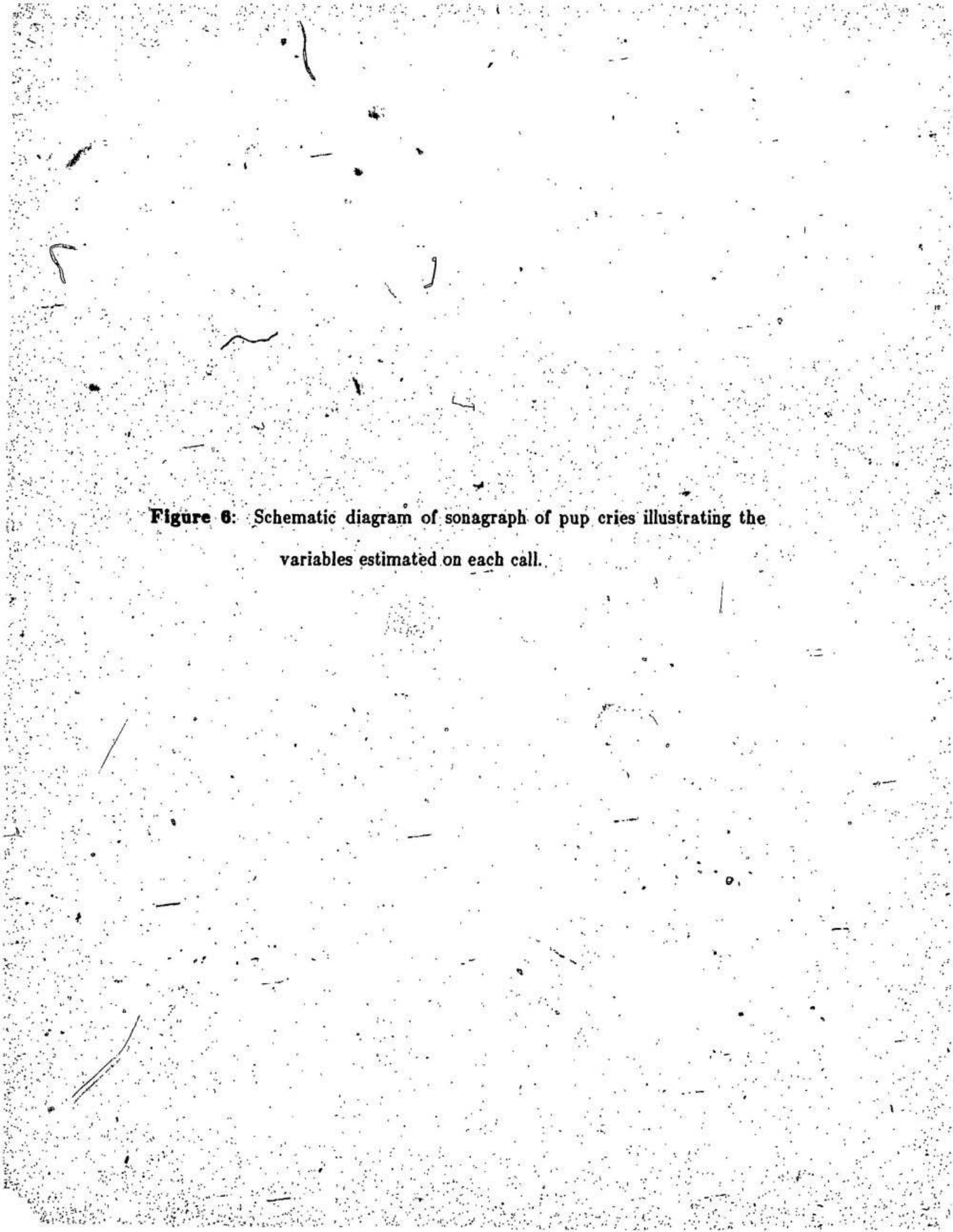


Figure 6: Schematic diagram of sonagraph of pup cries illustrating the variables estimated on each call.

FREQUENCY
TIME
HARMONIC RISE
HARMONIC INTERVAL
MAJOR HARMONIC
INTERCALL INTERVAL
DURATION OF CALL

3. **Number of harmonic bands** within each call.

4. **Number of harmonic bands missing in a call**; in the airborne call, any harmonics which were missing between the fundamental and highest band. For underwater calls, those bands absent when compared with their aerial versions plus the missing harmonics common to both.

5. **Major harmonic** of each call; the most intense harmonic band (frequency was measured at the mid-point of the major harmonic at its peak).

6. **Harmonic interval**; the interval separating the mid-point at the peak of two adjacent harmonic bands within a call.

7. **Harmonic rise**; the range of frequency modulation within each harmonic band measured between the lowest mid-point and the mid-point at the peak of the harmonic. The average harmonic rise was calculated for each call.

8. **Frequency modulation**; a rate calculated for each call by dividing the average harmonic rise by the time interval between the onset and the peak of the harmonic bands.

Approximately 250 bouts of simultaneous aerial and underwater calling were recorded. From these, all calls that were not clearly recognizable as coming from identified pups were eliminated from the analyses. The remaining 72 separate bouts were collected on 19 different days. A total of 848 calls were analyzed, of which 425 were recorded in air and 423 underwater. Since it was impossible to avoid recording the same pups on different days and pups could not be identified over days, it was necessary to treat each observation day separately; all comparisons between pups were conducted for each day. Every day the pups were consecutively numbered as they were recorded and their locations constantly monitored so that they would not be recorded as different individuals on that day. All analyses were run using the *SPSSx* (1983) statistical packages.

CHAPTER THREE: RESULTS

Description of pup calls

The pups called in bouts which contained from one to twenty-six individual calls ($\bar{x}$=5, s=4.03). The duration of each call varied about a mean of 0.31 sec. (s=0.14) with an average inter-call interval of 2.29 sec. (s=2.70). Each call contained from one to twelve parallel harmonic bands ($\bar{x}$=4.4, s=2.33) occurring between 50 and 4,150 Hz, all having the same basic inverted "v" shape (Figure 7).

Comparison of aerial and underwater calls

There were a number of significant differences, over all pups, between the simultaneously emitted aerial and underwater calls (for examples see Figure 7; statistics are summarized in Table I). The duration of the aerial calls ($\bar{x}$=0.34 sec) was significantly greater than the underwater versions ($\bar{x}$=0.28 sec). The mean major harmonic frequencies of airborne calls ($\bar{x}$=420.9 Hz) were significantly lower than the underwater calls ($\bar{x}$=927.2 Hz). A significant number of the lower harmonic bands present in aerial calls ($\bar{x}$=0.59) were missing from their underwater versions ($\bar{x}$=2.63) leading to a lower number of harmonics in those recorded underwater. The average harmonic interval was, therefore, greater in underwater calls (air, $\bar{x}$=459.4 Hz; water, $\bar{x}$=534.7 Hz). The average harmonic rise was higher in aerial calls (air, $\bar{x}$=214.5 Hz; water, $\bar{x}$=183.3 Hz). Frequency modulation within the calls and inter-call interval were the only variables which did not differ significantly between the two media.

Figure 7: Typical sonagraphs of two different pups' cries emitted simultaneously in air and underwater.

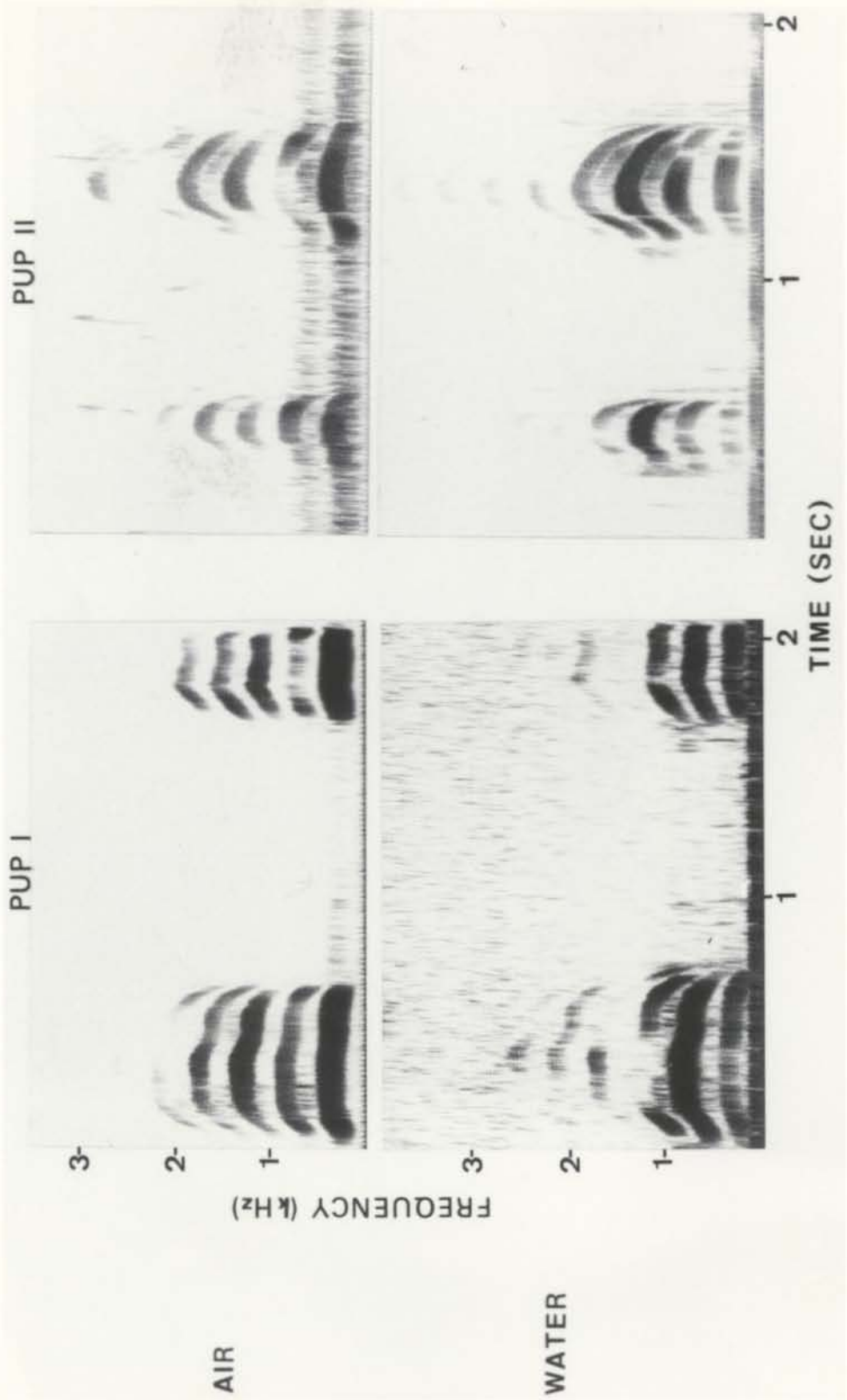

PUP I
PUP II
AIR
WATER
FREQUENCY (kHz)
3
2
1
TIME (SEC)
1
2

TABLE I: OVERALL COMPARISONS OF AERIAL AND UNDERWATER PUP CALLS ON SIX CHARACTERISTICS

CALL CHARACTERISTIC	AERIAL MEAN	UNDERWATER MEAN	ANALYSIS OF VARIANCE
Major harmonic (Hz)	420.90	927.21	$F_{1,823}=237.38$*
Number of Harmonics	5.24	3.51	$F_{1,846}=134.07$*
Harmonic Interval (Hz)	459.41	534.68	$F_{1,812}=25.56$ *
Number of Missing Harmonics	0.59	2.63	$F_{1,692}=223.09$*
Average Harmonic Rise (Hz)	214.49	183.28	$F_{1,800}=14.21$ *
Average Frequency Modulation (Hz/sec.)	1417.91	1420.85	$F_{1,800}=0.00$
Duration of Call (sec)	0.34	0.28	$F_{1,846}=30.98$ *
Inter-call Interval (sec)	2.15	2.43	$F_{1,669}=1.76$

* represents a significance level of $p < 0.05$.

Comparisons among pups

As mentioned previously, it was necessary to analyze each day separately since pups could not be identified from day to day and, therefore, it was impossible to discern whether animals had been recorded from in an earlier session. In order to ascertain whether the voices of the pups were individually distinct, physical call characteristics were compared among pups on each day, for each medium. Analysis of variance (ANOVA) was used to test differences between pups for those variables which had real number values (call duration, inter-call interval, major harmonic, harmonic interval, harmonic rise, and frequency modulation) while the count variables, which probably had a skewed distribution (number of harmonics and number of missing harmonics), were tested using Chi-squared. These analyses revealed the following differences (Table II; refer to Appendices for daily mean values and summaries of statistics for each variable in separate media for all pups).

Pups differed most on the basis of their mean major harmonic frequencies in both air and underwater (on 62.5 percent of the days pups were significantly different on the basis of this characteristic in air; on 50.0 percent of the days for the underwater calls). Duration of the aerial calls differed significantly on 62.5 percent of the days while this variable differed on 43.8 percent of the days in underwater calls. The number of harmonics present in the airborne calls was significantly different among pups on 37.5 percent of the days while the number present in the underwater versions was different on 56.3 percent of the days.

TABLE II: PERCENTAGE OF DAYS ON WHICH AMONG-PUP COMPARISONS OF CALL CHARACTERISTICS WERE SIGNIFICANTLY DIFFERENT IN EACH MEDIUM

CALL CHARACTERISTIC	MEDIUM AIR	WATER
Major harmonic (Hz)	62.5	50.0
Duration of Call	62.5	43.8
Number of Harmonics	37.5	56.3
Number of Missing Harmonics	43.8	31.3
Average Harmonic Rise (Hz)	43.8	31.3
Average Frequency Modulation (Hz/sec)	43.8	31.3
Harmonic Interval (Hz)	43.8	25.0
Inter-call Interval	31.3	18.8

The number of missing harmonics, the average harmonic rise and the frequency modulation were different for the same number of days for airborne and underwater calls (air, 43.8 percent; water, 31.3 percent). Pups were significantly different on the basis of harmonic interval in air (43.8 percent of the days) and water (25.0 percent of the days). Inter-call interval for both media was found to be significantly different on few days (air, 31.3 percent; water, 18.8 percent).

Post-hoc comparisons (see Appendices for Scheffé contrasts) revealed that on each day not all pups were significantly different from each other on a consistent combination of variables. Therefore the relative importance of a particular variable or combination of them was difficult to assess. For this reason a discriminant analysis was run using all variables but inter-call interval and call duration. The former proved to be unimportant by the ANOVAs and the latter because differences in the durations were thought to relate to behavioural measures and, therefore, could confound individual voice differences.

A discriminant analysis was run on six pup call characteristics (major harmonic, number of harmonics, number of missing harmonics, harmonic interval, harmonic rise and frequency modulation), separately for each medium, each day, to determine if the call characteristics could be used in combination to distinguish between pups. The significant discriminant functions, with the six remaining variables, were consistently able to account for a minimum of 78 percent (Table III) of the variation among pups; these functions performed as well as or better than the major harmonic used alone. The only days on which a reliable discriminant function could not be generated were those on which there were three or fewer pups or when there was an average of less than five calls per pup.

TABLE III: RESULTS OF DISCRIMINANT ANALYSIS INCLUDING POOLED WITHIN-GROUPS CORRELATIONS BETWEEN CANONICAL DISCRIMINANT FUNCTIONS AND DISCRIMINATING VARIABLES.

					VARIABLES					
	DAY	FUNCTION NUMBER	EIGEN VALUE	PERCENT VARIANCE	MAJOR HARMONIC	NUMBER OF HARMONICS	MISSING HARMONICS	HARMONIC INTERVAL	HARMONIC MODUALTION	FREQUENCY MODULATION
AIR	10	1	3.134	41.74	0.564	0.876	-0.169	-0.132	0.263	0.198
		2	2.735	36.42	0.601	-0.424	0.040	0.168	-0.081	-0.008
	13	1	87.759	96.90	0.914	-0.011	-0.040	0.091	0.161	0.043
	14	1	0.994	82.69	0.456	0.045	0.032	0.611	0.370	0.247
	15	1	5.121	62.24	0.860	0.300	0.176	0.224	0.029	-0.308
		2	2.723	33.09	0.510	0.135	0.175	0.067	0.600	0.930
	17	1	7.624	93.88	0.367	-0.270	--	0.203	0.225	0.324
WATER	10	1	2.722	58.92	0.241	0.526	0.497	0.055	0.272	0.085
		2	1.074	23.25	0.378	-0.489	0.083	-0.183	0.461	0.415
	13	1	11.116	64.21	-0.027	-0.615	0.242	0.154	0.208	0.326
		2	3.485	20.13	0.751	0.127	0.358	0.055	-0.232	0.432
	14	1	2.472	89.64	0.811	-0.161	0.388	0.309	0.323	0.300
	15	1	13.942	79.00	-0.350	0.460	-0.360	0.023	-0.005	-0.140
	17	1	12.109	91.87	0.689	-0.520	0.309	0.042	0.021	0.051

The pooled within-groups correlations between the canonical discriminant functions and discriminating variables indicated that the major harmonic of the airborne calls was weighted most heavily in four of the seven discriminant functions (see Table III). The discriminant functions describing the underwater cries correlated with either major harmonic or the number of harmonics in the calls. In both media the remaining variables were used to a lesser extent in creating the functions and none failed the tolerance tests ($p < 0.01$).

Behaviour

Pups started to call when they were on average 1 meter (s=1 meter) from their mothers. Mothers most frequently approached or stopped and waited for their calling pups (81 percent of the time), initiated nose-to-nose contact (99 percent of the time) and then continued to the haul-out site. Typically, pups then stopped crying (97 percent of the time) and followed their mothers after a nose-to-nose contact. Where no nose-to-nose contact occurred the pup was equally likely to continue calling, as not, while following its mother.

Pups were separated into two groups on the basis of distance from their mothers at the time of calling. Those pups less than two meters were categorized as near to their mothers while the remaining young, composed almost entirely of lone pups except for one which was three meters from its mother and another five meters from its mother, were far (two meters or more). The near pups had a significantly higher aerial major harmonic, inter-call interval and number of missing harmonics. The far pups had a significantly higher major harmonic and number of harmonics in their underwater calls and significantly more harmonics missing in their airborne cries (Table IV).

TABLE IV: SUMMARY TABLE OF MEANS AND STATISTICAL TEST RESULTS COMPARING CALL CHARACTERISTICS OF PUPS GROUPED ACCORDING TO DISTANCE FROM THEIR MOTHERS AT THE TIME OF CALLING

CALL CHARACTERISTIC	DISTANCE FROM MOTHER NEAR (< 2 m)	FAR (> 2 m)	TEST STATISTIC
AIR			
MAJOR HARMONIC	499.1	378.1	$F_{1,416}=13.38$ *
INTER-CALL INTERVAL	2.7	1.9	$F_{1,337}=7.69$ *
NUMBER OF HARMONICS	4.7	5.6	$\chi^2=13.53$ * N=425
NUMBER OF MISSING HARMONICS	0.8	0.5	$\chi^2=5.49$ * N=347
WATER			
MAJOR HARMONIC	807.1	992.9	$F_{1,405}=9.63$ *
NUMBER OF HARMONICS	3.2	3.7	$\chi^2=4.86$ * N=423

* represent a significance level of $p < 0.05$

Pup calls were then grouped according to the position of their mothers' heads (refer to Figure 5, page 16) at the time of calling. The underwater cries of pups calling to completely submerged mothers had a significantly higher major harmonic, harmonic rise and number of harmonics than those of pups calling to mothers in position 2 (Table V). They also had a significantly lower harmonic interval than pups calling to mothers in position 1 and 2. The aerial calls of these pups had significantly more missing harmonics than the pups calling to position 2 mothers.

The final grouping of pups was on the basis of mothers' responses to their calling pups (approaching the pup, stopping to wait for the pup, or no apparent response). In the aerial calls there were significantly more harmonics for the group whose mothers stopped and waited for them than for those whose mothers ignored them (Table VI). There were significantly more harmonics missing and the harmonic interval was higher in the underwater calls of pups whose mothers stopped and waited for them than for those whose mothers ignored them. Significantly more harmonics were present in the underwater cries of pups whose mothers approached them than ignored them.

TABLE V: SUMMARY TABLE OF MEANS AND STATISTICAL TEST RESULTS COMPARING CALL CHARACTERISTICS OF PUPS GROUPED ACCORDING TO POSITION OF THE MOTHERS' HEAD AT THE TIME OF CALLING

CALL CHARACTERISTIC	POSITION OF MOTHERS HEAD 1	2	3	TEST STATISTIC	SCHEFFÉ
AIR					
HARMONIC INTERVAL	474.2	473.3	433.3	$F_{2,190}=3.41$	
NUMBER OF MISSING HARMONICS	0.8	0.4	1.1	$\chi^2=11.62$ N=151	
WATER					
MAJOR HARMONIC	720.6	612.2	994.1	$F_{2,195}=15.66$	3 > 2
HARMONIC INTERVAL	763.1	592.6	453.3	$F_{2,182}=8.05$	3 < 1,2
HARMONIC RISE	179.4	155.7	196.9	$F_{2,187}=3.66$	3 > 2
NUMBER OF HARMONICS	3.5	2.9	3.9	$\chi^2=13.92$ N=205	

Note: all of the above comparisons were significant at $p < 0.05$ level

KEY TO POSITIONS OF MOTHER'S HEAD:
1 COMPLETELY VISIBLE
2 PARTIALLY SUBMERGED
3 COMPLETELY SUBMERGED

TABLE VI: SUMMARY TABLE OF MEANS AND STATISTICAL TEST RESULTS COMPARING CALL CHARACTERISTICS OF PUPS GROUPED ACCORDING TO MOTHERS' RESPONSE TO CALLING

CALL CHARACTERISTIC	RESPONSE OF MOTHERS 1	2	3	TEST STATISTIC	
AIR					
NUMBER OF HARMONICS	4.7	5.4	4.0	$\chi^2=7.53$	N=204
WATER					
HARMONIC INTERVAL	496.9	607.9	446.1	$F_{2,194}=3.69$	
NUMBER OF HARMONICS	3.9	3.4	2.9	$\chi^2=6.50$	N=217
NUMBER OF MISSING HARMONICS	1.9	3.9	1.5	$\chi^2=14.44$	N=169

NOTE: all of the above comparisons were significant at $p < 0.05$ level

KEY TO RESPONSES:

1 MOTHER APPROACHED CALLING PUP
2 MOTHER STOPPED TO WAIT FOR CALLING PUP
3 MOTHER CONTINUED AS BEFORE, APPARENTLY IGNORING PUP

CHAPTER FOUR: DISCUSSION

Unlike those pinnipeds which give birth to their pups on land, *Phoca vitulina concolor* regularly follow their mothers into the water for the first few weeks of life. The precocity of the young permits this species to use haul-out sites which are often only accessible at low tide. It also enables mother-pup pairs to escape disturbances, such as vehicle and boat traffic, which occur frequently at many pupping sites (Venables and Venables, 1955; Curry-Lindahl, 1975; Renouf et al., 1981). However, this mobility requires that at least one member of the pair must recognize the other to remain in contact during the four week nursing-period. Maintaining contact could be particularly difficult when the pair is in the water due to the increased motility of the young combined with poor visibility in turbid waters, strong currents and the masking effects of high ambient noise levels (Renouf, 1980).

The pups show a strong tendency to follow their own mothers (Lawson, 1983) and Renouf (1984) has suggested that a mother might be able to monitor her pup's movements behind her by localizing its calls. Thus, she would know when her offspring was not following as it should and could then respond appropriately. Although the closest pup should be her own, there are occasions, such as during disturbances, when many young can be calling at once from very similar positions. At these times, it would be advantageous for the mother to recognize her offspring's voice. If the mother could distinguish her offspring's calls from those of nearby young, the time necessary for her to locate her own pup would be reduced. This could be crucial when factors, such as the ever present strong currents, also increase the likelihood of separation.

Individual variation

Mother-infant vocal recognition has been postulated for most of the otariid species of pinnipeds (Marlow, 1975; Ono, 1972; Peterson and Bartholomew, 1969; Stirling and Warneke, 1971; Trillmich, 1981; Vaz-Ferreira and Achaval, 1979). Vocal recognition has also been suggested to occur in several phocid pinnipeds, such as northern elephant seals (Petrinovich, 1974), grey seals (Fogden, 1971), and possibly harp seals (Terhune et al., 1979) and harbour seals (Renouf, 1984).

The results of the present study confirm Renouf's (1984) finding that pups differed primarily on the basis of their fundamental frequency (referred to as major harmonic in this work). The discriminant analysis, similar to that used by Antonelis and York (1985) to identify individual male northern fur seals by their vocalizations, indicated that the number of harmonics, frequency of major harmonic, harmonic interval, number of missing harmonics, average harmonic rise and average frequency modulation, in combination, could reliably distinguish among all pups (except on those days when less than three pups were included in the analyses). The pooled within-groups correlations between the canonical discriminant functions and the discriminating variables signify that the major harmonic of the airborne calls was consistently important in distinguishing between calls of different pups. Discrimination among pups on the basis of underwater cries was most strongly influenced by either the major harmonic or the number of harmonics present in the calls. The remaining variables fluctuated in their relative importance to the daily discriminant functions. However, none of

them failed the tolerance test and, therefore, were not eliminated from the analysis. This suggests that all of the variables contributed to the differences between pups. That is, pups appear to have unique voices which the mothers could use to distinguish their offspring from others. Renouf (1985) was able to demonstrate that a captive, adult female harbour seal could distinguish between several different pup calls. It is possible this female was using the aforementioned physical call characteristics to make this discrimination.

Comparison of aerial and underwater calls

Renouf (1984) found that pup calls were transmitted simultaneously in air and underwater when the pup's head was in air. The present study found that there were significant differences in the physical characteristics of the aerial and underwater versions of these calls. Typically, lower harmonics in the underwater call were missing, leading to a greater harmonic interval, and the major harmonic frequency was higher than in the aerial calls.

There are no other reports of simultaneous call production in two media by pups of other phocids. However, there are several studies comparing adult vocalizations in the two media. The California sea lion emits barks and clicks simultaneously in both media when its body is submerged and its head is out of the water. Schevill, Watkins and Ray (1963) found no physical differences between these two versions when they examined calls from captive *Zalophus*. As they suggested, the holding tanks were reverberating concrete pools which could have caused behavioural changes in sound production. Sufficiently loud recordings were only obtained when the animals were within two meters of the

hydrophone which might have lead to a cross over of the signal, from air to water, a problem which could occur in any of the work with captive animals. Schusterman and Balliet (1969) found no difference in the male California sea lion bark when simultaneous aerial and underwater phonations were compared [comparing calls produced when the head was in air and the throat (propagator) was submerged]. Slight differences between aerial vocalizations of male pups and underwater calls of adult male hooded seals (*Cystophora cristata*) were suggested by Terhune and Ronald (1973). Unfortunately, they were unable to compare calls produced by the same individuals in each medium. One might expect to find differences in frequencies between animals of such different sizes, simply on the basis of disparity in size of the sound generating organs and air passages.

The differences in aerial and underwater vocalizations reported in the present study are not likely to solely reflect differences in transmission properties of the two media. It is likely that the distance between any of the young and the hydrophone (three to ten meters) was too small to allow for frequency and amplitude changes in the cries as they passed through water. Normally, one would expect higher frequency bands of underwater calls to be most affected by the reflective properties of the surface of the water and to be attenuated more rapidly than lower frequency bands. Since air and water have different impedance characteristics the interface would serve as a large obstacle. As sound waves propagate near the air/water interface, some high frequency bands with short wavelengths would reflect and cancel while others would be reinforced (Wiley and Richards, 1978). Instead, the present study found more lower bands were missing in underwater calls. The channel in which recording took place was

shallow (maximum depth of three meters) which could prevent transmission of the lower, longer-wavelength, frequencies because the wavelengths could be longer than the surface-to-bottom distance. However, one might expect the major harmonic to be eliminated if this occurred. The shift of emphasis to higher frequency bands in the underwater calls is difficult to explain. Perhaps it was a product of some type of resonance effect of the seal's lung cavity, like those produced by the pharyngeal pouches in the walrus (*Odobenus rosmarus*) on their bell-like sounds (Fay, 1960b, 1979; Schevill, et al., 1966). If the resonant frequency of the lung cavity were such that it equalled a particular harmonic of the vocalization then the amplitude of that band might be enhanced as it passed through the chest. This same effect might cause a shift in emphasis from one frequency in air to another underwater if the route of propagation were different between the media (passing straight into the air from the sound generating organs compared to passing down through the lungs and into the water). Simultaneously, lower harmonics may have been filtered as the sound passed through the thick blubber and skin into the water. Perhaps these layers act as high-pass filters which selectively allow high frequencies to pass unaffected while reducing the amplitude of the low-frequency harmonics. Therefore, the potential augmenting resonance effect of the lung cavity and the filtering properties of the blubber may explain the significant differences in pup calls between the two media.

The discriminant analysis indicated that pups had unique calls in air and underwater. Therefore, mothers could distinguish the cries of their young from other pups on the basis of either version. The masking effects of high ambient

noise levels could make it difficult for a mother to hear her offspring's aerial calls. Since seals are on average 15 dB more sensitive to sounds underwater than in air (Møhl, 1968) she could rely on the simultaneously produced underwater cries, in this situation, to recognize her pup. In any case, with two renditions of the call available to the mother, she could theoretically attend to the call in the quieter medium.

The physical differences between the airborne and underwater calls give the mothers two different pieces of information. Like all binaural animals, harbour seals are able to localize sound sources. By comparing differences in time of arrival, and possibly intensity and phase, of a sound to each ear they can detect an angular separation of two sound sources in air (minimum audible angle [MAA]) as small as 3° (click stimulus; Terhune, 1974). This is only slightly less accurate than humans who have a MAA of 1° in air (Mills, 1958). Hence, a mother seal would normally be able to locate her offspring on the basis of airborne calls. A calling pup should be more difficult to locate underwater since seals have a MAA of 9° (click stimulus; Terhune, 1974) in that medium. However, seals are better able to locate an underwater sound source than untrained humans who have a MAA of 11° (pulsed white noise stimulus; Feinstein, 1975).

The harbour seal receives aerial information through the auditory meatus while underwater signals are received just ventral to the meatal orifice and pass to the inner ear through a vertical bar of tissue approximately seven centimeters in length (Møhl and Ronald, 1975). It seems likely then, that the female harbour seal would be able to hear both the aerial and underwater call at the same time if her head is placed such that the water line is just ventral to the meatal orifice, as suggested by Renouf (1984).

Since sound travels four times faster through water than air, the underwater calls of the pups would arrive at the mothers' ears before the airborne ones. Thus, as a pup fell further behind its mother the difference in time of arrival between the air and water calls would increase, informing the mother of the increasing distance between herself and her pup. Furthermore, a mother could detect differences of intensity, phase and time of arrival simultaneously within air or underwater calls, thereby adding a fourth dimension to the binaural comparison. Therefore, it might be possible for the mothers to integrate the localization cues provided in the air and underwater calls simultaneously to locate their young in the three-dimensional environment they occupy while swimming.

Behaviour

Analysis of variance of physical call characteristics between pups calling in different behavioural contexts indicated that the distance of the pup from its mother, the position of the mother's head at the time of calling, and the mother's response were important variables. The mean aerial major harmonic, inter-call interval and number of missing harmonics were higher for pups close to their mothers while the number of harmonics was significantly less than for pups 2 meters or more from their mothers. The pups calling far from their mothers had a significantly higher underwater major harmonic and more harmonics than the near pups. These findings might reflect the motivational state of the pups at the time of calling. It appears that 2 meters (approximately 1.3 seal lengths) might be a critical distance for the young. It is possible that at this distance, and beyond, pups are unable to recognize their mothers from other seals with certainty and,

therefore, are unsure of their mothers' location. Perhaps this would be stressful and cause the pups to put more energy into their cries which should lead to more harmonic bands being present in the calls and might also account for the higher major harmonics. These distance-related differences might serve to inform the mother of her pup's confusion or stress which should encourage her to approach her pup and reassure it of her identity through nose-to-nose contact.

There were also significant differences in the call characteristics between pups calling to completely submerged mothers and those calling to mothers with their heads visible at the surface. The mean aerial harmonic interval was less while there were more harmonics missing in the cries of pups calling to submerged mothers than mothers that were partially visible. The mean underwater major harmonic, harmonic rise and number of harmonics were also higher for pups crying to submerged mothers than for pups calling to partially visible mothers. Also, the former had a significantly lower harmonic interval than the pups calling to either partially or completely visible mothers. Again, these differences might reflect the stress level or motivational state of the young at the time of calling. It is likely that a pup at the surface would be more stressed when it was unable to see its mother than if it could. Overall, these differences in calls might serve to inform the mother that, firstly, her offspring had surfaced and, secondly, it needed to see her in order to continue following.

Analysis of variance of call characteristics among pups grouped according to their mothers' responses revealed several significant differences. In air, the mean number of harmonics of pups whose mothers stopped to wait for them was higher than for those pups whose mothers appeared to ignore their calls. The pups

whose mothers stopped to wait for them also had a higher harmonic interval and more missing harmonics in their underwater cries than the apparently ignored pups. The pups whose mothers approached them had significantly more harmonic bands than the calls of pups whose mothers waited for, or ignored, them. It is difficult to clearly determine the causal relationship in these groupings. Presumably the pups who were ignored should be more stressed than those whose mothers waited for them. The physical call differences between pups whose mothers ignored them and those whose mothers responded (either by approaching or stopping to wait for the pups) might indicate that the ignored pups were uncertain as to which seal was mother and, therefore, were unsure toward whom they should direct their calls. A response by a seal, most likely mother, could serve to encourage a pup to direct and emphasize its calls. However, it seems more probable that the differences in calls might inform the mother as to the well-being of her pup such that cries with fewer harmonics might be produced by a less stressed pup which doesn't require immediate attention from its mother.

These findings support Lawson's (1983) suggestion that both members of the pair take an active role in maintaining contact with the other, but when in danger of separation the mother takes overt control over keeping the pair together. This study presents the possibility that it is the information in the vocalizations of the pup which inform the mother of an increasing risk of separation.

Conclusions

A comparative examination of pup recognition mechanisms in various pinniped species indicates that there are differences between the otariids and the

phocids. Most species of otariids, which have extremely long nursing periods (Galápagos sea lions will nurse as long as three years; Trillmich, 1981), must leave the young unattended, often for several days, while they search for food. Upon return, the mothers can locate their offspring by waiting for the offsprings' individual vocal responses to their PACs. The phocids have relatively short lactation periods (there is evidence that hooded seal young are weaned in four days; Bowen, et al., 1985) which reduces the total amount of time over which mothers must leave their offspring alone. Also, many of them birth in groups with lower densities than those of otariids. Since it is difficult to study many of the phocids, little is known about their pup-recognition mechanisms although Terhune et al. (1979) suggest that a vocal mechanism is unlikely in harp seals. Perhaps the pupping site density differences provide an explanation for the apparently poorly developed vocal recognition in the ice breeding species. This becomes evident when grey seals and elephant seals are considered. These species, compared to other phocids, have equally short nursing periods (approximately three weeks) but they maintain the highest density groups, among phocids, at pupping time and the females do make use of PACs. It is possible that there are selective pressures to develop vocal recognition in species with high density rookeries. This suggestion could be tested by examining the walrus which also has dense nursing groups and is thought to nurse for two years (Fay, 1982). There are data which indicate that walrus calves have distinctive bark trains (Miller, 1985) but vocal recognition has yet to be studied. The results of this study indicate that harbour seals, which pup in higher densities than ice-breeding phocids, but more dispersed than grey seals and elephant seals, have developed a

recognition mechanism to ensure mothers and pups stay together despite the presence of other pairs nearby.

Harbour seals gather into rookeries and have short lactation periods. The adults do not have a PAC, but the pups have a vocal signature which their mothers can recognize. Further, harbour seal mothers can rely on different aspects of their pups' behaviour to ensure that the pair stays together. In fact, the harbour seal is unusual in that the young follow their mothers into the sea from birth. Therefore, it is important that the mothers recognize the cry of their offspring and be able to use the continual calling as a means to locate them. The uniqueness of the calls facilitates both recognition and localization.

Earlier work has indicated that mother-pup pairs are able to remain together, despite the mobility of the young and the difficult environmental factors, through a following tendency of the pups. Evidence indicates that maternal effort is increased when the risk of separation is great, such as when pairs are in the water, through obvious efforts to minimize the intrapair distance. Differences in physical features of the vocalizations were found to occur in conjunction with distance from mother, position of the mother's head at the time of calling and the mother's response. This implies that some of the onus was on pups to alert their mothers to potential danger of separation through differences in their calls as a result of increased stress. Thus, a mother could decrease the danger of separation when she was informed by her pup that the youngster could not follow as it should, thereby ensuring that the pair remained in close contact.

Future Considerations

While this study includes extensive call data and behavioural measures not previously documented, there are several potential improvements which could be implemented. Firstly, and of greatest importance, a marking program would greatly enhance the accumulation of useful vocalization data. This would allow for a comparison of call characteristics over the nursing period for known individuals to determine if there are developmental changes in calling as weaning approaches. Secondly, a tagging program would make playback studies possible.

We have been extremely wary of approaching mothers with newborns as the likelihood of separation might be high. Thus, we cannot tag mothers early enough to have marked individuals throughout the short, four week nursing period. Therefore, playback studies have been impossible. If adult females could be marked after their offspring have been weaned we would have known individuals to work with in the following year. This would facilitate the collection of calls from known pups which could be played back to their mothers as well as strangers.

Unfortunately, there would be the added problem of interpreting mothers' responses to recorded calls in a playback study. Since females do not vocalize in response to their pups' cries it would be necessary to measure their reactions to the sound source. Responses to calls from a speaker in an unexpected location might not include the behaviours of waiting or approaching normally seen between mothers and pups.

Recordings of pup vocalizations from the surface of the young's body would

assist in determining the physical effects of the body on the underwater calls. Research of this nature would allow for more certainty as to whether the variation in physical call characteristics between the media are a result of transmission properties of water, or the pup's anatomy.

REFERENCES

Antonelis, G.A., Jr., and A.E. York. 1985. Identification of individual male northern fur seals, *Callorhinus ursinus*, from their vocalizations. *Sixth Bien. Conf. Biol. Mar. Mamm. Abstracts.* Vancouver, B.C..

Bartholomew, G.A., and N.E. Collias. 1962. The role of vocalization in the social behaviour of the northern elephant seal. *Anim. Behav.*, **10**:7-14.

Bonner, W.N.. 1981. Grey seal, *Halichoerus grypus* Fabricius, 1791. *in Handbook of Marine Mammals.* (S.H. Ridgway and R.J. Harrison, eds.), Academic Press Inc., New York, New York. pp. 111-144.

Bowen, D.L., D.J. Boness and O.T. Oftedal. 1985. Morphometric changes during lactation and weaning in hooded seal mothers and their pups. *Sixth Bien. Conf. Biol. Mar. Mamm. Abstracts.* Vancouver, B.C..

Burns, J.J.. 1981. Ribbon seal, *Phoca fasciata* Zimmermann, 1783. *in Handbook of Marine Mammals.* (S.H. Ridgway and R.J. Harrison, eds.), Academic Press Inc., New York, New York. pp. 89-110.

Curry-Lindahl, K.. 1975. Ecology and conservation of the grey seal *Halichoerus grypus*, common seal *Phoca vitulina*, and ringed seal *Pusa hispida* in the Baltic Sea. *Rapp. P.-v. Reun. Cons. int. Explor. Mer.*, **169**:527-532.

Fay, F.H.. 1960b. Structure and function of the pharyngeal pouches of the walrus (*Odobenus rosmarus* L.). *Mammalia*, **24**:361-371.

Fay, F.H.. 1979. Walrus *Odobenus rosmarus* (Linnaeus, 1758). *in Handbook of Marine Mammals.* (S.H. Ridgway and R.J. Harrison, eds.), Academic Press Inc., New York, New York. pp. 1-23.

Fay, F.H.. 1982. Ecology and biology of the Pacific Walrus, *Odobenus rosmarus divergens* Illiger. *North American Fauna*, **74**:1-279.

Feinstein, S.H.. 1975. The accuracy of diver sound localization by pointing. *Undersea Biomedical Research*, **2**:173-184.

Fogden, S.C.L.. 1971. Mother-young behaviour at Grey seal breeding beaches. *J. Zool., Lond.*, **164**:61-92.

Frost, K.J., and L.F. Lowry. 1981. Ringed, Baikal and Caspian seals - *Phoca hispida, Phoca sibirica* and *Phoca caspica*. *in Handbook of Marine Mammals.* (S.H. Ridgway and R.J. Harrison, eds.), Academic Press Inc., New York, New York. pp. 29-54.

Lawson, J.W.. 1983. Behavioural adaptations by harbour seal mothers and pups to an amphibious lifestyle. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Newfoundland, Canada.

Le Boeuf, B.J., R.J. Whiting and R.F. Gantt. 1972. Perinatal behavior of northern elephant seal females and their young. *Behavior*, **34**:121-156.

Ling, J.K., and M.M. Bryden. 1981. Southern elephant seal *Mirounga leonina*. *in Handbook of Marine Mammals*. (S.H. Ridgway and R.J. Harrison, eds.), Academic Press Inc., New York, New York. pp. 297-327.

Mansfield, A.W. and B. Beck. 1977. The grey seal in eastern Canada. Dept. Fish. Env. Fisheries and Marine Service Tech. Rep. 704.

Marlow, B.J.. 1975. The comparative behaviour of the Australasian sea lions *Neophoca cinerea* and *Phocarctos hookeri* (Pinnipedia: Otariidae). *Mammalia*, **39**:159-230.

Miller, E.H.. 1985. Airborne acoustic communication in the walrus *Odobenus rosmarus*. *National Geographic Research*, **1**:124-145.

Mills, A.W.. 1958. On the minimum audible angle. *J. Acoust. Soc. Am.*, **30**:237-246.

Møhl, B.. 1968. Hearing in seals. *in The Behavior and Physiology of Pinnipeds*. (R.J. Harrison, R.C. Hubbard, R.S. Peterson, C.E. Rice and R.J. Schusterman, eds.), Appleton-Century-Crofts, New York, New York. pp. 172-195.

Møhl, B., and K. Ronald. 1975. The peripheral auditory system of the harp seal *Pagophilus groenlandicus* (Erxleben,1777). *Rapp. P-v. Reun. Cons. int. Explor. Mer.*, **169**:635-637.

Ono, K.A.. 1972. Mother-pup interactions in the steller sea lion (*Eumetopias jubata*). *Proc. Ninth Ann. Conf. Bio. Sonar Diving Mammals*, 9-20.

Peterson, R.S. and G.A. Bartholomew. 1969. Airborne communication in the California sea lion, *Zalophus californianus*. *Anim. Behav.*, **17**:17-24.

Petrinovich, L.. 1974. Individual recognition of pup vocalization by the northern elephant seal mothers. *Z. Tierpsychol.*, **34**:308-312.

Ralls, K., P. Fiorelli, and S. Gish. 1985. Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. *Can. J. Zool.*, **63**:1050-1056.

Renouf, D.. 1980. Masked hearing thresholds of harbour seals (*Phoca vitulina*) in air. *J. Aud. Res.*, **20**:263-269.

Renouf, D.. 1984. The vocalization of the harbour seal pup (*Phoca vitulina*) and its role in the maintenance of contact with the mother. *J. Zool., Lond.*, **22**:583-590.

Renouf, D.. 1985. A demonstration of the ability of the harbour seal *Phoca vitulina* (L.) to discriminate among pup vocalizations. *J. Exp. Mar. Biol. Ecol.*, **87**:41-46.

Renouf, D. and M.B. Davis. 1982. Evidence that seals may use echolocation. *Nature*, **300**:635-637.

Renouf, D., L. Gaborko, G. Galway, and R. Finlayson. 1981. The effect of disturbance on the daily movement of harbour seals and grey seals between the sea and their hauling grounds at Miquelon. *Applied Animal Ethology*, **7**:373-379.

Schevill, W.E., W.A. Watkins and C. Ray. 1963. Underwater sounds of pinnipeds. *Science*, **141**:50-53.

Schevill, W.E., W.A. Watkins and C. Ray. 1966. Analysis of underwater *Odobenus* calls with remarks on the development and function of the pharyngeal pouches. *Zoologica*, **51**:103-111.

Schusterman, R.J., and R.F. Balliet. 1969. Underwater barking by male sea lions (*Zalophus californianus*). *Nature*, **222**:1179-1181.

Schusterman, R.J., R.F. Balliet and S.St. John. 1970. Vocal displays under water by the gray seal, the harbor seal, and the steller sea lion. *Psychon. Sci.*, **18**:303-305.

SPSSx User's Guide. 1983. SPSS Inc. and McGraw-Hill Book Co., New York. pp. 287-299, 431-436, 453-461, 671-695.

Stirling, I. and R.M. Warneke. 1971. Implications of a comparison of the airborne vocalizations and some aspects of the behaviour of the two Australian fur seals, *Arctocephalus* spp., on the evolution and present taxonomy of the genus. *Aust. J. Zool.*, **19**:227-241.

Terhune, J.M.. 1974. Directional hearing of a harbour seal in air and water. *J. Acoust. Soc. Am.*, **56**:1862-1865.

Terhune, J.M. and K. Ronald. 1973. Some hooded seal (*Cystophora cristata*) sounds in March. *Can. J. Zool.*, **51**:319-321.

Terhune, J.M., M.E. Terhune and K. Ronald. 1979. Location and recognition of pups by adult female harp seals. *Appl. Anim. Ethol.*, **5**:357-380.

Trillmich, F.. 1981. Mutual mother-pup recognition in Galápagos fur seals and sea lions: Cues used and functional analysis. *Behaviour*, **78**:21-42.

Vaz-Ferreira, R. and F. Achaval. 1979. Relacion y reconocimiento materno- filial en *Otaria flavescens* (Shaw) "lobo de un pelo", y reacciones de los machos subadultos ante los cachorros. *Acta zool. lilloana, Tucuman, Argentina*, **35**:295-302.

Venables, U.M. and L.S.V. Venables. 1955. Observations on a breeding colony of the seal *Phoca vitulina* in Shetland. *Zool. Soc. Lond. Proc.*, **125**:521-532.

Wiley, R.H., and D.G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.*, **3**:69-94.

Appendix 1a: Mean major harmonic value of AIR calls for individual pups on each day.

	PUP NUMBER										df	F	Scheffé
DAY	1	2	3	4	5	6	7	8	9	10			
1	350.0	382.8									1,7	0.33	
2		512.5	781.8	297.5							2,26	7.48	* 3 differs from 4
3		183.3	425.0	575.0	200.0	770.5	675.0	557.8	272.5		7,41	3.15	* 6 differs from 9
4	300.0	437.5	337.5	250.0	212.5						4,9	21.21	* 5 differs from 2,3
													2 differs from 4
5	200.0	675.0									1,11	8.00	*
8	1433.3												
10	508.3	237.5	1164.6	658.3	485.0	262.5	325.0	1120.0	283.3	284.1	9,58	9.32	* 3 and 8 differ
													from 1,6,7,9,10
11	1329.2	216.7	375.0								2,9	272.92	* 1 differs from 2,3
12	343.8	391.7	585.0								2,9	1.18	
13	280.0	262.5	1043.8	225.0	233.3	237.5					5,22	376.12	* 3 differs from all
14	150.0	325.0	229.2	500.0							3,33	2.86	
15	220.0	307.5	316.7	377.3	297.9						5,30	0.91	
16	350.0												
17	344.4	791.7	225.0	227.5							2,24	9.04	* 2 differs from all
18	285.0	248.4	315.6								2,18	3.65	* 2 differs from 3
19	282.5	550.0	237.5								2,18	3.46	
20	257.8												
21	225.5	216.7									1,6	0.02	
22	255.4	275.0	187.5								2,11	11.13	* 3 differs from 1,2

* represents $p < 0.05$

Appendix 1b: Mean major harmonic value of WATER calls for individual pups on each day.

	PUP NUMBER										df	F	Scheffé
	1	2	3	4	5	6	7	8	9	10			
DAY													
1	387.5	353.0									1,12	0.56	
2	359.4	1295.8	1292.7								2,19	7.40	* 1 differs from 2,3
3	1347.2	743.8	1081.3	958.3	1450.0	1012.5	946.9	1225.0	1121.2		8,62	2.77	*
4	1335.0	975.0	1087.5	1111.1	1200.0						4,32	0.84	
5	810.0	1250.0									1,5	1.27	
8	1450.0												
10	450.0	750.0	266.1	291.7	753.1	562.5	503.4	691.7	716.7	840.9	9,60	3.46	*
11	1393.8	1225.0	1700.0								2,4	0.87	
12	1400.0	1475.0	1737.5								2,9	3.74	
13	1285.0	2800.0	1825.0	1725.0	1407.1	1831.3					5,20	6.15	* 2 differs from 1,5
14		409.4	242.2	1026.9							2,22	19.86	* 5 differs from 3,4
15	983.3	187.5	754.2	475.0	800.0	350.0					5,13	5.73	* 1 differs from 2
16	414.3												
17	1427.5	1016.7	1175.0	219.6							3,12	23.46	* 4 differs from all
18	518.2	396.9	591.7								2,22	0.38	
19	1184.4	725.0	378.1								2,15	5.19	* 1 differs from 3
20	728.1												
21	1360.0	1412.5									1,7	0.02	
22	2100.0	1833.3	409.4								2,8	3.99	

* represents $p < 0.05$

Appendix 2a: Mean harmonic modulation of AIR calls for individual pups on each day.

	PUP NUMBER										df	F	Scheffé
	1	2	3	4	5	6	7	8	9	10			
DAY													
1	670.0	291.6									1,7	23.07 *	
2	254.3		274.5	145.8							2,29	2.73	
3		175.0	305.3	262.5	125.0	140.0	87.5	213.0	251.1		7,37	3.96 *	6 differs from 9
4	100.0	93.8	192.3	83.3	148.9						4,10	3.16	
5	162.5	188.6									1,11	0.32	
8	201.7												
10	216.2	150.0	301.8	129.2	222.2	78.1	147.9	278.0	316.7	282.1	9,58	3.02 *	
11	200.7	135.4	272.2								2,9	1.44	
12	115.4	261.1	339.2								2,9	12.15 *	1 differs from 3
13	225.0	246.6	366.7	300.5	153.7	118.9					5,21	2.44	
14	164.6	215.8	178.1	254.7							3,31	1.35	
15	125.7	128.3	270.9	220.8	241.3	354.3					5,30	4.20 *	6 differs from 1,2
16	206.9												
17	230.8	322.5	173.5	153.6							3,24	3.23 *	2 differs from 4
18	191.7	224.6	269.5								2,17	0.34	
19	199.1	87.5	191.2								2,18	1.04	
20	140.4												
21	138.6	102.8									1,6	0.23	
22	216.8	286.9	115.1								2,11	4.83 *	2 differs from 3

* represents $p < 0.05$

Appendix 2b: Mean harmonic modulation of WATER calls for individual pups on each day.

	PUP NUMBER										df	F	Scheffé
	1	2	3	4	5	6	7	8	9	10			
DAY													
1	271.8	261.6									1,12	0.05	
2	292.3		343.5	216.9							2,19	3.80	* 3 differs from 4
3	273.2	139.1	230.9	149.3	150.0		137.2	282.9	343.1		7,54	6.13	* 9 differs from 2,7
4	168.8	120.1	316.7	210.4	221.1						4,28	1.11	
5	183.8	160.9									1,5	0.38	
8	194.4												
10	191.9	237.5	151.5	147.2	215.5	100.0	144.7	112.5	310.0	220.8	9,57	3.04	*
11	176.1	308.4	118.8								2,4	1.37	
12	122.2	270.8	63.0								2,8	1.20	
13	345.0	170.3	52.8	225.0	178.2	72.9					5,19	7.64	* 1 differs from 3,6
14	75.0	77.1	56.3	169.2							3,23	3.66	* 4 differs from 3
15	128.1	50.0	179.2	133.3	83.3	81.3					5,12	2.02	
16	132.7												
17	110.4	135.0	75.0	97.0							3,15	0.51	
18	182.2	112.5	102.8								2,21	1.40	
19	111.5	50.0	84.4								2,15	0.43	
20	82.3												
21	204.5	219.8									1,7	0.04	
22		58.3	50.0								1,5	1.43	

* represents $p < 0.05$

Appendix 3a: Mean frequency modulation of AIR calls for individual pups on each day.

	PUP NUMBER										df	F	Scheffé
	1	2	3	4	5	6	7	8	9	10			
DAY													
1	6700.0	1556.7									1,7	143.40 *	
2		1594.3	1643.4	1169.5							2,29	2.83	
3		1750.0	2482.7	1312.5	1000.0	1223.3	583.3	1867.4	1396.9		7,37	1.49	
4	933.4	937.5	1207.5	666.7	691.6						4,10	1.08	
5	976.2	1304.9									1,11	0.87	
8	1344.5												
10	1458.5	857.1	1435.8	1275.0	1044.8	712.5	1097.7	1841.8	1624.0	1548.0	9,58	2.18 *	
11	1314.3	503.5	1828.7								2,9	3.83	
12	492.9	1440.1	2202.8								2,9	25.13 *	1 differs from 2,3
13	1485.2	1532.2	1960.2	1869.8	668.3	838.5					5,21	2.85 *	
14	1270.9	1921.7	1613.9	1777.5							3,31	0.43	
15	1296.3	875.0	1587.0	1050.0	1829.3	2700.2					5,30	5.38 *	6 differs from 1,2
16	1352.3												
17	1799.4	2350.5	1030.0	931.4							3,24	7.31 *	2 differs from 4
18	1225.7	1446.4	1682.3								2,17	0.39	
19	1239.2	875.0	1053.7								2,18	0.76	
20	888.5												
21	855.6	638.9									1,6	0.82	
22	1537.5	1554.4	708.3								2,11	9.93 *	3 differs from 1,2

* represents $p < 0.05$

Appendix 3b: Mean frequency modulation of WATER calls for individual pups on each day.

	PUP NUMBER										df	F	Scheffé
	1	2	3	4	5	6	7	8	9	10			
DAY													
1	785.8	1460.7									1,12	2.48	
2	1425.0		1675.6	1276.4							2,19	0.78	
3	3295.8	897.4	1767.7	972.2	1500.0		1016.2	2864.8	1852.6		7,54	3.52 *	
4	1225.0	703.6	1266.7	1712.6	1383.6						4,28	0.43	
5	1310.5	1220.9									1,5	0.04	
8	1655.6												
10	1439.6	1187.5	789.7	1069.5	979.8	920.9	843.4	695.8	1611.7	1207.3	9,57	2.73 *	
11	1432.3	944.5	2375.0								2,4	1.56	
12	892.6	1979.2	2776.7								2,8	4.20	
13	3225.0	3406.3	1055.6	2133.4	868.4	1020.8					5,19	12.60 *	1 differs from 3,5,6
													2 differs from 3,5,6
14	1000.0	908.3	867.2	1559.6							3,23	1.75	
15	1281.3	333.3	1395.8	1333.3	1666.7	1187.5					5,12	2.11	
16	1219.0												
17	1729.2	1850.0	750.0	702.4							3,15	4.60 *	
18	1101.0	1712.5	1013.9								2,21	0.90	
19	947.9	1000.0	812.5								2,15	0.23	
20	864.6												
21	1530.8	1516.5									1,7	0.00	
22		1833.3	791.7								1,5	26.27 *	

* represents p < 0.05

Appendix 4a: Mean harmonic interval in AIR calls for individual pups on each day.

	PUP NUMBER										df	F	Scheffé
	1	2	3	4	5	6	7	8	9	10			
DAY													
1	400.0	472.8									1,7	7.43 *	
2		418.8	481.0	425.4							2,29	3.32	
3		433.3	480.0	368.8	425.0	476.3	420.0	521.4	518.8		7,41	0.79	
4	450.0	1231.3	516.1	425.0	410.4						4,10	6.86 *	2 differs from all
5	437.5	420.5									1,11	0.14	
8	352.5												
10	572.0	466.7	437.0	425.0	452.7	404.2	432.3	347.3	475.4	429.7	9,57	3.43 *	1 differs from 8
11	573.6	416.7	529.2								2,9	4.33 *	1 differs from 2
12	390.6	515.5	498.7								2,9	5.53 *	
13	503.3	374.4	576.3	415.5	418.8	439.6					5,22	6.00 *	3 differs from 4,5
14	442.5	427.8	410.2	476.8							3,33	4.03 *	3 differs from 4
15	422.4	449.2	515.0	422.2	478.0	538.6					5,30	2.05	
16	404.8												
17	389.0	439.8	424.8	378.5							3,24	2.72	
18	515.8	440.9	439.6								2,18	2.00	
19	487.4	458.3	452.7								2,18	0.68	
20	534.4												
21	426.7	443.1									1,6	0.05	
22	458.9	412.6	327.4								2,11	3.60	

* represents $p < 0.05$

Appendix 4b: Mean harmonic interval in WATER calls for individual pups on each day.

	PUP NUMBER										df	F	Scheffé
	1	2	3	4	5	6	7	8	9	10			
DAY													
1	331.3	461.5									1,12	11.08 *	
2	407.0		406.6	530.8							2,20	2.20	
3	443.5	397.4	416.5	335.2	412.5	570.8	459.6	493.9	473.7		8,63	2.31 *	
4	628.1	317.3	535.0	434.9	418.9						4,32	4.87 *	1 differs from 2,5
5	432.9	395.0									1,5	0.65	
8	458.3												
10	416.7	466.7	445.1	494.5	426.5	408.3	420.5	325.0	447.5	429.6	9,53	0.52	
11	545.8	393.8	562.5								2,3	5.50	
12	563.9	495.8	481.9								2,10	0.28	
13	430.0	415.6	600.0	591.7	422.9	654.2					5,17	1.60	
14	587.5	429.7	678.9	625.3							3,24	1.25	
15	437.5	333.3	400.7	529.2	700.0	689.6					5,11	1.61	
16	853.2												
17	527.1	458.3	675.0	522.3							3,13	0.78	
18	480.6	1879.2	1003.1								2,18	28.59 *	2 differs from 1,3
19	1035.7	450.0	1095.8								2,11	1.08	
20	732.8												
21	453.4	407.1									1,7	0.70	
22	847.9	400.0	386.5								2,7	4.17	

* represents $p < 0.05$

Appendix 5a: Mean number of harmonics in AIR calls for individual pups on each day.

	PUP NUMBER										N	χ^2	
DAY	1	2	3	4	5	6	7	8	9	10			
1	5.0	4.6									9	0.75	
2		3.9	5.6	3.1							32	15.62	*
3	1.0	2.0	5.8	5.0	4.0	4.2	6.0	3.5	5.9		50	25.63	*
4	2.0	3.0	2.0	3.0	3.8						15	9.37	*
5	2.5	3.8									13	3.32	
8	7.7												
10	3.1	4.0	5.3	3.0	4.6	2.0	3.1	9.8	4.2	7.2	69	52.54	*
11	4.2	3.3	3.3								12	3.04	
12	4.3	3.0	4.8								12	3.66	
13	3.6	6.5	5.3	7.3	5.8	5.0					28	8.55	
14	7.0	5.0	5.8	6.8							37	5.68	
15	4.8	3.4	3.2	5.7	3.3	5.2					36	13.20	*
16	7.7												
17	8.7	8.2	9.3	10.6							28	13.06	*
18	6.6	6.0	5.6								21	0.77	
19	6.1	4.7	4.6								21	1.84	
20	5.3												
21	8.6	4.7									8	2.72	
22	8.4	5.3	5.5								14	5.18	

* represents $p < 0.05$

Appendix 5b: Mean number of harmonics in WATER calls for individual pups on each day.

	PUP NUMBER										N	χ^2	
DAY	1	2	3	4	5	6	7	8	9	10			
1	3.5	5.3									14	3.95	*
2	4.0		5.3	3.5							23	9.02	*
3	2.6	4.5	3.8	5.7	3.0	2.8	3.9	3.2	5.4		72	41.02	*
4	2.8	6.5	3.5	4.9	5.1						38	11.26	*
5	4.8	4.0									7	0.66	
8	5.0												
10	1.9	4.0	3.3	3.7	2.8	2.5	2.4	2.0	2.7	3.4	71	22.86	*
11	2.4	5.0	3.0								8	3.14	
12	2.3	2.8	3.8								14	5.84	*
13	2.2	4.5	1.7	2.0	4.7	2.0					27	20.42	*
14	3.0	2.8	2.5	2.5							29	1.61	
15	2.7	1.8	3.0	2.3	1.7	2.5					20	5.99	
16	5.1												
17	2.3	1.6	3.0	2.0							19	12.19	*
18	4.6	2.0	2.0								25	11.63	*
19	2.1	1.5	2.3								18	1.62	
20	2.0												
21	7.8	7.5									9	0.02	
22	3.3	2.0	3.8								11	3.59	

* represents $p < 0.05$

Appendix 6a: Mean number of missing harmonics in AIR calls for individual pups on each day.

	PUP NUMBER										N	χ^2	
	1	2	3	4	5	6	7	8	9	10			
DAY													
1	0.0	0.6									9	0.75	
2			0.0	1.3							11	3.44	*
3	2.0	3.3	1.0	1.0	1.0	1.0	0.0	0.4	0.4		42	13.91	*
4	1.5	4.0	1.0	2.0	2.3						10	5.48	
5	1.5	0.5									4	1.50	
8	2.0												
10	0.1	0.0	0.0	1.0	0.2	1.3	0.0	0.0	0.3	0.0	67	25.82	*
11	1.0	1.0	1.0								8	0.06	
12	1.0	1.7	0.6								12	3.91	
13	0.6	1.8	0.0	0.0	1.8	0.6					26	10.77	*
14	0.0	0.6	0.0	0.0							29	4.80	
15	0.0	0.0	0.3	0.0	0.3	0.5					23	5.60	
16	0.6												
17	0.0	0.0	0.0	0.0							26	0.00	*
18	0.2	0.8	0.3								19	1.73	
19	0.0	0.0	0.9								20	7.06	*
20	0.6												
21	1.4	5.0									8	3.32	*
22	0.4	1.3	0.0								14	3.68	

* represents $p < 0.05$

Appendix 6b: Mean number of missing harmonics in WATER calls for individual pups on each day.

	PUP NUMBER										N	χ^2	
DAY	1	2	3	4	5	6	7	8	9	10			
1	0.0	0.0									14	0.00	
2	0.0		3.0	1.2							14	8.73	*
3	1.0	0.0	2.8	0.0	2.0	1.5	3.0	0.9	1.4		42	11.89	
4	1.0	1.0	0.0	0.3	1.0						14	3.37	
5	0.0	0.5									4	1.00	
8	3.0												
10	1.3	0.0	2.2	0.3	1.8	0.8	0.7	7.5	1.7	4.0	66	33.25	*
11	2.4	0.0	2.0								8	4.52	*
12	2.8	2.3	1.2								12	7.95	*
13	2.2	3.5	3.7	6.3	1.3	3.4					26	15.07	*
14	5.0	2.8	3.9	4.5							29	4.88	
15	3.7	1.8	1.0	3.3	2.0	2.8					20	5.29	
16	3.6												
17	6.3	6.8	7.0	7.4							19	2.67	
18	3.2	5.0	4.2								25	1.54	
19	4.3	4.0	3.3								18	1.11	
20	2.8												
21	2.4	1.3									8	0.73	
22	4.8	4.3	1.8								11	5.13	

* represents $p < 0.05$